STRUCTURAL PARALLELISM BETWEEN SPORE-FORMS IN THE ASCOMYCETES[1]

C. R. Orton

(With Plate 152, Containing 7 Figures)

The term "structural parallelism" is here substituted for the word "homology" which was used when the paper was first presented. There was some objection to the use of the word *homology* and with good reason, for although Brefeld appears to have used the word in a somewhat similar manner, the general use of this conception has been, especially in zoology, not a structural or functional resemblance but a phylogenetic similarity of origin. The similarity which the writer wished to bring out in this paper might be more nearly expressed by the word *analogy* but this implies a functional similarity which, although it may be present, is not precisely what is in mind.

The term *physiological parallelism* was suggested as the general one used to describe similarities like those enumerated in this paper. It seems, however, that even this expression is not strictly appropriate, for the word physiological implies again a functional relationship.

The relationship which the writer has in mind is one of a purely structural nature between ascospores and conidia in certain species of Ascomycetes, though similarity in color often accompanies it. Considering the subject purely from this standpoint, the term *structural parallelism* would seem to fit more closely the phenomenon which the writer desires to express in this paper. This appears to be the first time that a study has brought facts of this sort together for this class of fungi, although such a relation undoubtedly has been observed by other investigators.

We are indebted to Tulasne for the early researches among the

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Ascomycetes in which he demonstrated the pleomorphic condition of this class. His researches were based upon the comparison of many forms, their co-habitation, anatomy, and the alternation of their spore-forms. In this way he was able to work out the alternate asexual stages of a number of Ascomycetes.

It may be mentioned that as a result of Tulasne's work a storm of controversy developed which lasted for some time. On the one hand, pleomorphy was considered ridiculous by the most conservative botanists of the time, while on the other hand his results led men of overenthusiasm to ridiculous conclusions.

Owing to the importance of this group on account of its large number of species and their common association with plant diseases, it has occurred to the writer that any constant similarity existing between the conidial and ascigerous stages which might enable an investigator to conclude with some degree of certainty whether two stages are related would be of great assistance. This information would be all the more valuable provided that it was of such a nature that it might be ascertained by a comparative study of the spores.

While the author[2] was working upon the correlation existing between certain species of rusts his attention was first called to the similarity between conidia and ascospores of certain species of Ascomycetes, the genetic connection of which has been demonstrated. This paper is the result of observations and notes taken from time to time upon such species as may be said to show structural parallelism between their conidia and ascospores.

A similar parallelism between certain spore-forms in the Uredinales has been pointed out by Arthur[3], who worked out the connection existing between *Aecidium verbenicola* and *Puccinia Vilfae*,[3] *Aecidium Traxini* and *Puccinia peridermiospora*,[4] and *Aecidium Cephalanthi* and *Puccinia Seymouriana*.[5] He compared the peculiar morphology of the aeciospores with the same peculi-

[2] Orton, C. R., Correlation between certain species of *Puccinia* and *Uromyces*. Mycologia 4: 194–204. 1912.

[3] Arthur, J. C., Cultures of Uredineae in 1899. Bot. Gaz. 29: 268–276. 1900.

[4] Arthur, J. C., The Uredineae occurring upon *Phragmites*, *Spartina*, and *Arundinaria* in America. Bot. Gaz. 34: 1–20. 1902.

[5] Arthur, J. C., loc. cit.

arity possessed by the urediniospores of suspected alternate species and proved by cultures that his presumptions were correct.

It has been pointed out by de Bary[6] and others that certain species of Ascomycetes on which both conidial and ascigerous stages are known produce mycelium of "the same qualities and capabilities" from both kinds of spores.

There is frequent allusion to this in mycological literature where physiological studies of the mycelium arising from the conidia of a species have been compared with the mycelium arising from ascospores of the known or suspected alternate stage. In one case which has come to my attention a dissimilarity in this respect was considered of sufficient importance to warrant keeping them separated. This view is certainly a safe one to follow, but no one yet has proved in a sufficiently large number of cases that the mycelia from both spores are identical in a physiological test, such as is made in culture media, to justify final conclusions. Such an identity is possible and, if actual, would prove a valuable test to further substantiate the theory of parallelism as herein indicated.

The following examples will serve to bring out more clearly what the writer has in mind. The powdery mildews show this parallelism in every case with which the writer is familiar. Here, there is in the asexual stage the production of simple, colorless, more or less barrel-shaped conidia corresponding almost in every detail with the ascospores of the connected stge.

In the genera *Rhytisma* and *Lophodermium,* which have the conidial forms *Melasmia* and *Leptostroma* respectively, the same likeness is found. In both, the conidia and ascospores are simple, colorless, and cylindrical. The genus *Glomerella* possesses two conidial stages, *Gloesporium* and *Colletotrichum,* each of which possesses conidia structurally similar to the ascospores of *Glomerella.* Still more striking is the similarity between the ascospores of *Ophionectria coccicola* E. & E. and the conidia of its alternate stage, *Microcera* sp. Both conidia and ascospores are fusoid, colorless, and many-celled. (Fig. 1.)

Herprotrichia nigra has brown, two- to three-septate ascospores

[6] De Bary, A., Morphology and Biology of the Fungi, Mycetozoa and Bacteria (English edition), pp. 225–230. 1887.

which are so like the conidia of the fungus that if a conidium and ascospore were placed side by side they could hardly be told apart.

Such examples might be multiplied many times but only a few more need be enumerated. *Gnomonia, Pseudopeziza, Sclerotinia, Botryosphaeria, Guignardia, Cryptosporella* and others further considered possess this same parallelism.

One might say that the rule does not hold in certain genera of the Sphaeriaceae where the ascospores are two-celled and the conidia of the alternate stage one-celled. This may be explained in all the cases with which the writer is familiar when one observes the germination of the conidia. For example, the conidia of *Endothia parasitica* are unicellular but germinate and produce mycelium from both ends. Eventually, there are four germ-tubes produced, two from each end of the conidium. This is exactly what happens when the ascospore germinates, two germ-tubes being derived from each cell of the ascospore.[7] (Fig. 2.) At the beginning of the germination, the conidium sometimes assumes almost the exact shape of the two-celled ascospore of the fungus. However, the interesting condition remains that, so far as germination is concerned, the pycnospores are parallel with the ascospores.

Another condition exists commonly among the species which possess pleomorphic conidial stages, where, of course, one would expect to find only one of the conidial forms similar to the ascospores. Such a species as *Curcurbitaria Laburni* may be cited here. This species is said to have three types of conidia produced successively in pycnidia of varying form. The first two of these conidial stages produce spores which bear no resemblance to the ascospores, but the third and last conidia produced are almost exactly like the ascospores, which are brown and pluricellular-compound. (Fig. 3.) In this case, as well as in genera like

[7] Anderson, P. J., and Rankin, W. H. Endothia Canker of Chestnut. Cornell Agric. Exp. Sta. Bulletin 347: 566–567. 1914. Since this paper was read, the bulletin cited here has appeared. The action of the nuclei during this process of germination can hardly be as Anderson and Rankin have stated, that "the nuclei pass out into the germ tubes almost as soon as they start." If this were literally true, only two germ-tubes could be derived from one spore, as there would be no nuclei left in the spore to give rise to the two later germ tubes which are developed. Evidently, the writers meant to convey the idea that those nuclei which pass out into the tubes do so immediately.

Pleospora and *Apiosporium,* the likeness between the conidia in one stage and the ascospores is very striking.[8] (Fig. 4.)

A variation of the cases just mentioned, and one which might appear to be an exception, exists in several genera as *Venturia* and *Plowrightia* where the ascospores are two-celled and the conidial stages often unicellular but occasionally two-celled like the ascospores. (Fig. 6.) It might be said here that the mere production of occasional two-celled conidia seems to be of sufficient importance to prove the parallelism, but it is to be noted also that the one-celled spores germinate at both ends and thus function in the same way as does its two-celled companion. This makes the evidence doubly strong that the relationship between conidia and ascospores is very close.

As I have already pointed out, it is manifestly impossible for more than one of the conidial forms of pleomorphic species to be structurally parallel with its ascospores.

Accepting the pleomorphic character of a considerable number of Ascomycetes and allies, why is it not logical to suppose that this condition may be typical of the class and where it fails to appear it may be accounted for by the hypothesis that one or more stages have been lost during the evolution of the group? A majority of the apparent discrepancies in the parallelism of conidia and ascospores may be explained on the supposition that the conidial stages corresponding to the ascospores of the species have been suppressed. This might well be true in such a family as the Hypocreaceae where some of the most apparent incongruities appear. In this family, we find such species as *Nectria galligena, N. discophora,* and *Hypomyces Ipomoeae,* in which there is no such manifest similarity. On the other hand, however, in this same family, such species as *Gibberella Saubinetii, Ophionectria coccicola,* and *Calonectria graminicola* present striking parallelisms. (Fig. 7.)

[8] Higgins, B. B. Contribution to the Life History and Physiology of *Cylindrosporium* on Stone Fruits. Am. Jour. Bot. 1: 145–173. 1914. Higgins presented at the same meeting at which this paper was read a very interesting case of parallelism in the genus *Coccomyces,* which he has proved to be the ascigerous stage of *Cylindrosporium.* The genus appears to be pleomorphic, at least some species possess three spore stages besides the ascospores. Of the conidial stages, only the *Cylindrosporium* stage appears to function as infection spores and these are almost identical with the ascospores. (Fig. 5.)

There are three possible explanations for these exceptions. *First*, as has just been mentioned, the life history may have become shortened or it may be incompletely known. From the survey of the studies made, this appears to be the most probable condition existing where parallelism fails to appear. *Second*, the supposed conidial and ascigerous stages of a species may have no connection. Numerous instances have been brought to light which show that the original work on the basis of which genetic relationships have been accepted was erroneous. Undoubtedly there are many such assumed connections in this class of fungi. *Third*, the hypothesis falls down completely in certain cases.

While it cannot be said, with our present knowledge of many of the Ascomycetes, that all cases can be made to conform to this theory, yet there seems to be enough evidence presented to show that such a distinct similarity is the rule and that dissimilarity is the exception.

Summarizing these observations, it would seem that among the strictly monomorphic conidial forms of Ascomycetes a rather constant parallelism exists between conidia and the ascospores of the alternate stage; that when one- and two-celled conidia occur, as in *Venturia* and other genera, the ascospores of the alternate stage are generally two-celled; that when the conidia are one-celled and the ascospores two-celled the conidia may in some cases behave as a two-celled spore when they germinate.

Among the pleomorphic conidial species the same likeness probably exists between one of the conidial stages and the ascospores of the alternate stage. Further, it seems probable that when parallelism fails to appear it may be due to abbreviation or to our incomplete knowledge of their life history.

A study of the nuclear phenomenon of the conidial stages during spore formation and germination would undoubtedly throw much light upon the whole subject.

The important feature of parallelism as herein outlined is the assistance given the mycologist and plant pathologist to anticipate with some accuracy the probable relationship between conidial and ascosporic stages.

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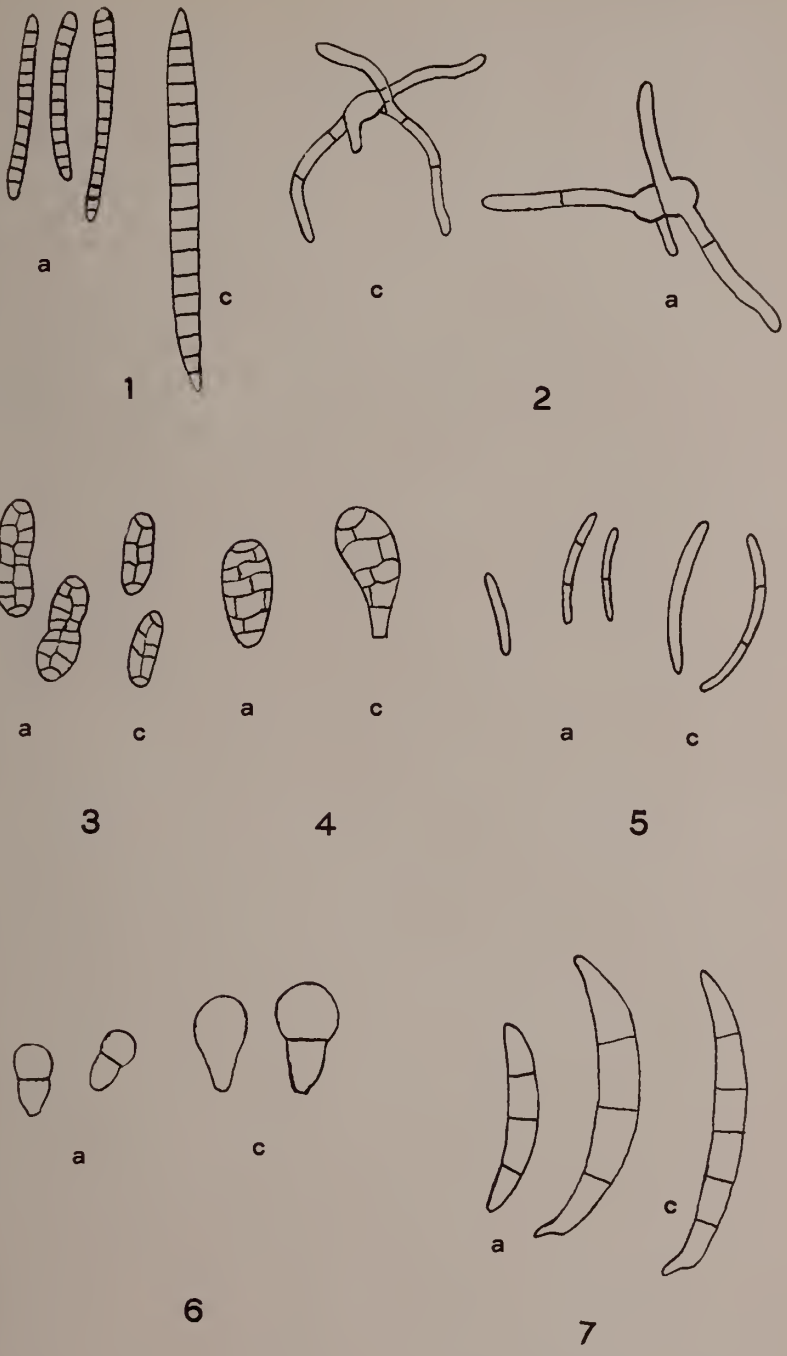

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